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Current Opinion in Insect Science

Evolution of geographic variation in thermal performance curves in the face of climate change and implications for biotic interactions

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We review the recent literature on geographic variation in insect thermal performance curves (TPCs). Despite strong thermal differences, there is often no change in TPCs across geographic gradients. When shifts occur, these are mostly vertical (indicating an overall shift in performance across temperatures, that is, countergradient or cogradient variation) and less horizontal (reflecting thermal adaptation). Based on this, using a space-for-time substitution approach, we generated likely evolutionary scenarios of TPC evolution to simulate the outcome of biotic interactions under future warming. We illustrate how taking evolution of the TPCs into account may strongly impact the predicted outcome of biotic interactions under climate warming. Importantly, both the type and the magnitude of the TPC shift was identified to be crucial to determine who will be winners and losers of biotic interactions.

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Current Opinion in Insect Science 2018, **29**:78–84

This review comes from a themed issue on **Global change biology**

Edited by **Oswald J Schmitz** and **Adam E Rosenblatt**

For a complete overview see the Issue and the Editorial

Available online 11th July 2018

https://doi.org/10.1016/j.cois.2018.07.004

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Introduction

Understanding how performance changes with temperature is crucial to assess the potential of populations to deal with current and future thermal regimes [1]. The relationship between a performance trait and temperature is known as the thermal performance curve (TPC). TPCs of insects typically have a rising part until the temperature where the best performance is reached (i.e. thermal optimum, or T_{opt}). Above this temperature, performance steeply decreases until reaching the critical thermal maximum (CT_{max}), where performance becomes zero (Figure 1).

Populations across geographic gradients may experience strongly different thermal regimes. This holds both at the macrogeographic scale, for example along latitudinal and altitudinal gradients, and at the microgeographic scale, for example along urbanization gradients [2]. As a result, TPCs can strongly depend on the populations' geographic origin [3]. Studying the evolution of TPCs across geographic gradients is getting renewed interest to predict responses to climate change [1,3]. Using a space-for-time approach [4], the current TPC at a warmer site can indeed be used as a proxy to predict the TPC at a colder site under a given warming scenario.

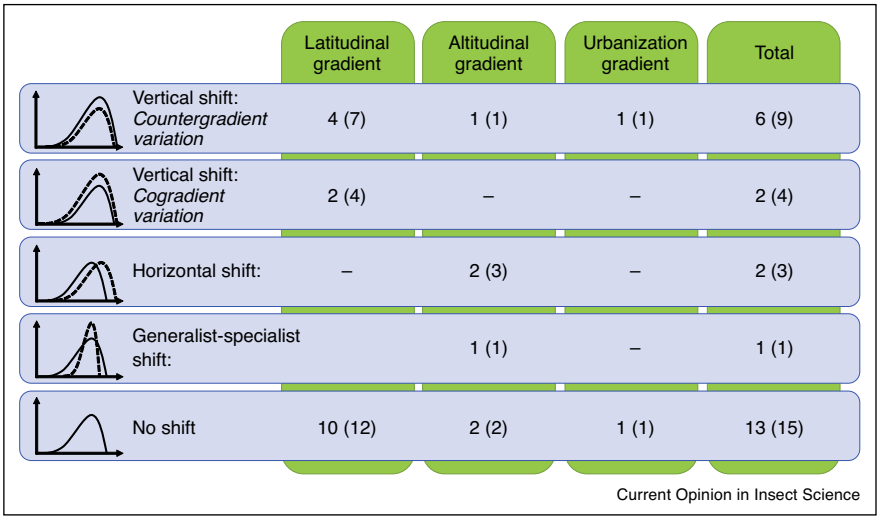
Although it is increasingly accepted that the fate of populations to persist locally depends not only the ability to deal with warming *per se*, but also on the ability to deal with biotic interactions under warming [5], this has been much less studied. Very few studies indeed directly addressed how biotic interactions change along temperature-associated geographic gradients (e.g. [6,7]). Importantly, the outcome of biotic interactions such as consumer–resource interactions [8–10] and interspecific competition [11,12] at a given temperature can be predicted based on the TPCs of the interacting species. For example, comparing the TPCs for swimming speed of a predator and its prey, the predator attack speed was found to be lower than the prey escape speed below a certain temperature, which was suggested to be the reason of the mostly unsuccessful predator attacks below that temperature [10]. Therefore, geographic patterns of TPCs of interacting species may inform on geographic patterns of their interaction, and using a space-for-time approach also on the evolution of biotic interactions under future warming.

We here review recent work on TPCs across geographic gradients in insects and describe emerging patterns. Based on this review we then generate hypothetical scenarios of evolutionary changes in TPCs of two interacting species to infer possible patterns in the outcomes of their interactions in the face of future warming. We particularly highlight how evolution of the TPCs, often ignored in such studies, may affect the predictions of the outcome of the interaction between species in the face of climate change.

General geographic patterns in TPCs

Shifts in ectotherm TPCs along geographic gradients can show three, not mutually exclusive, patterns [13] that are visualized in Figure 1:

Figure 1



Schematic overview synthesizing the documented shifts in thermal performance curves (TPCs) along geographic gradients in insects. Numbers outside brackets give the total number of studies reporting a certain shift, numbers within brackets give the total numbers of traits showing a certain shift. Note that several studies reported different mode of TPC shifts for different traits (measured in the same study), resulting in an inflated 'total' number of studies (i.e. the total number of studies included in this review was 18, instead of 24).

(i) A 'horizontal shift' occurs when warm/cold-adapted populations perform better at higher/lower temperatures. This pattern is often associated with local thermal adaptation, where the maximum performance is achieved at the temperature the population is adapted to (T_{opt}), and is driven by a trade-off between performance at higher and lower temperatures [14].

(ii) A 'vertical shift' occurs when populations outperform across temperatures. This may take two forms. The scenario where populations inhabiting colder regions outperform those from warmer regions is termed countergradient variation (CnGV), as the genetic influence opposes the influence of the thermal environment. This shift, often documented for growth or development rate, is associated with stronger time constraints experienced in colder environments [15,16]. The opposite scenario where warm-adapted populations outperform cold-adapted populations along the thermal gradient, is called cogradient variation (CoGV). Although the underlying drivers of this pattern are not clear, it is often detected for morphological traits [16].

(iii) A 'generalist-specialist shift' occurs when populations adapted to more stable thermal environments have a narrower thermal performance breadth (i.e. the temperature range where performance can occur) and higher maximum performance than populations adapted to more variable thermal environments [17,18]. This trade-off is suggested to be driven by structural constraints in the thermal flexibility and stability of enzymes [19].

Many studies have been testing geographic patterns in only the extreme values of the TPC: the minimum (CT_{min}) and the maximum (CT_{max}) temperature where performance becomes zero. Recent studies on insects confirm the general patterns that CT_{min} is lower in high-latitude than in low-latitude populations, while CT_{max} shows no or only a weak latitudinal pattern (reviewed in [20]; but see e.g. [21,22]). Along altitudinal gradients, the emerging pattern is that of a higher CT_{max} at warmer, lower altitudes, and vice versa for CT_{min} (e.g. [23,24]). It is important to note that the geographic patterns in the extremes of the TPC do not automatically inform about the type of shift in the entire TPC. For example, TPCs with a different CT_{max} may still have the same T_{opt} and vice versa.

Geographic patterns in insect TPCs

To identify geographic patterns in insect TPCs, we selected recent intraspecific studies with at least two geographically separated conspecific populations, that assessed performance at $\geq$3 constant temperatures (the minimum requirement for constructing TPCs). We follow the definition of performance traits as biological rate processes with a time-dependent component [25]. We specifically focused on performance traits directly relevant for the outcome of biotic interactions in the short term (within a generation), thereby excluding cross-generational numerical effects.

Specifically, we included individual growth rate, development time/rate, and consumption/feeding rate. We thereby make the reasonable assumption that higher values of these traits will make the organism better in dealing with a specific biotic interactor in the short term. For example, faster growing organisms in general do better in competitive interactions (e.g. [11]). Note that these performance traits do not necessarily translate into long-term fitness because of trade-offs [16]. We refer the reader to Table 1 for additional details of the selection criteria.

The selection criteria resulted in 18 insect studies (Table 1) dominated by two orders: lepidopterans (6 studies) and dipterans (4 studies). Development time and growth rate were by far the most frequently tested traits (17 studies). The majority of studies looked at macrogeographic gradients, mainly latitudinal (13 studies) and less frequently altitudinal gradients (2 studies), and only one study considered a microgeographic (urbanization) gradient. Two studies applied a mixed gradient, using populations that differed both in their latitudes and altitudes. These three gradients typically reflect temperature gradients with the higher temperatures at lower latitudes/altitudes, and at urban sites [2], causing plastic increases in the values of the studied performance traits.

Surprisingly, despite strong differences in thermal regimes, most studies revealed no change in TPCs across geographic gradients (Figure 1). The two reviews on geographic patterns in TPCs across all animals dealt either only with CnGV [15] or only with CnGV and CoGV patterns [16], hence cannot inform about the generality of the 'stasis' of TPCs. This lack of geographic signal may, however, partly reflect the often documented absence of latitudinal patterns in CT_{max} [20]. The absence of a strong latitudinal pattern in CT_{max} has been recently explained by interference from range expansion events, where insect species undergoing large-scale range expansions seem to show a latitudinal invariance of CT_{max} [26]. Other explanations for a lack of TPC shifts involve perfect compensation under CnGV resulting in no clinal trait variation (for body size TPCs: [16,27–29]), and too short time since the divergence of the study populations [30].

Among the insect studies where a geographic signal was detected, the most common pattern was a vertical shift in TPCs, whereas horizontal shifts were less prevalent. This is often suggested to be due to constraints on the physiological underpinnings of performance: horizontal shifts of TPCs require radical changes to the structural and physiological characteristics of enzymes, which is considered as an evolutionarily conserved system [13,31]. Vertical shifts, on the other hand, are primarily driven by up-regulation or down-regulation of enzymes, which is a more evolutionarily labile process [32]. Among the two vertical shift models, CnGV patterns were more common than CoGV patterns, in agreement with the findings of the review by Conover *et al.* [16] including also non-insect studies where CnGV was overwhelmingly dominant over CoGV (also for insects, 13 vs 2 studies: [16]). Notably, only one insect study reported a correlated change in TPC breadth and maximal performance along a geographic gradient, reflecting a generalist–specialist shift [33]. Yet caution is warranted, as reliable detection of this mode of TPC shift requires specific experimental and statistical designs, such as a temperature gradient spanning the entire thermal spectrum of the study organism, and explicitly measuring the trade-off between T_{opt} and thermal performance breadth.

Predicting interaction outcomes under future warming based on evolving TPCs

Differences in TPCs between two interacting species have been successfully used to predict the outcome of their pairwise interaction in the short term (e.g. [10]). Based on this, we hypothesize that patterns in TPCs along geographic gradients can be useful tools to predict how species interactions will change along these gradients. Moreover, we can use the TPC of a given species at the warmer site of a gradient to infer how the TPC at the colder site will evolve under future warming (i.e. space-for-time: [4]).

We simulated six scenarios how an evolutionary shift in the TPC of a species A (matching a current geographic TPC pattern) may shape the outcome of the interaction in the short term with a species B (Figure 2). Because no geographic shift in TPC was the most common geographic pattern detected in our literature review (Figure 1), we assume that the TPC of species B does not evolve. We based the evolution of the TPC of species A on the three most observed geographic shifts in insect TPCs (CnGV, CoGV, and horizontal shift); for each shift type we considered the effect of a moderate and a strong shift. In each scenario the current temperature at which both species interact is t1 and the future temperature under climate change is t2. In the current scenario (at t1) species A is superior compared to species B. Without evolution of the TPC, species A will, however, become inferior compared to species B under future warming at that site (at t2).

A first pair of evolutionary scenarios assumes a downward vertical shift (matching CnGV) of the TPC of species A. This will result in lower performance of species A under future warming, hence shifts the outcome of the interaction in favour of species B (Figure 2a). Note that in this case, evolution of the TPC of species A will be maladaptive in terms of the outcome of the interaction with species B. Increasing the magnitude of the downward vertical shift will further decrease the performance of species A (Figure 2d). On the other hand, when species A evolves an upward vertical shift (matching CoGV),

Table 1

Recent (last 5 years) studies testing for geographic patterns in insect thermal performance curves (TPCs). To infer the type of TPC shifts, we primarily relied on the authors' interpretation of the results. When not explicitly mentioned, we describe the pattern based on statistical results and visual inspection of the TPCs. We interpreted a significant main effect of geographic origin (e.g. latitude) as a signal of a vertical shift in TPCs. Depending on the alignment with the geographic gradient, the vertical shift was described as either counter-gradient variation (CnGV) or cogradient variation (CoGV). In case of a significant geographic origin × rearing temperature interaction, we checked whether the T_{opt} differed along the gradient, which would indicate a horizontal shift in TPCs. Finally, a negative correlation between T_{opt} and thermal performance breadth was interpreted as a shift in the TPC breadth (generalist-specialist shift). We excluded traits that did not show temperature dependency. When TPCs crossed, we considered this as an irregular pattern. When traits reacted to temperature but the TPCs did not shift along the geographic gradient, we indicated this as 'no shift'. We only included common-garden studies where animals from the different populations were reared from the egg stage, as TPCs from field-collected individuals cannot inform on the genetic basis of any potential shift

Group	Species	Trait	Gradient (no. of populations)	Geographic pattern	No. of temperatures	Reference
Collembola	*Folsomia quadrioculata*	Development time	Latitude (10)	No	3	[44]
Collembola	*Folsomia quadrioculata*	Growth rate (juvenile)	Latitude (5)	No	4	[45]
		Development time (age at first reproduction)		No		
Diptera	*Drosophila subobscura*	Development time (age at first reproduction)	Latitude (3)	No	3	[46]
Diptera	*Culex pipiens*	Development rate	Latitude/Altitude (4)	No	6	[47•]
Diptera	*Sepsis punctum*	Development rate	Latitude (3)	CnGV[a]	5	[31]
Diptera	*Sepsis thoracica*	Development time	Latitude (45)	CnGV	3	[29]
		Growth rate		CnGV		
Lepidoptera	*Ematurga atomaria*	Development time	Latitude/Altitude (4)	CnGV	3	[48]
		Growth rate		No		
Lepidoptera	*Bicyclus safitza*	Development time	Latitude (2)	Irregular	4	[49] (supplementary)
		Growth rate		Irregular		
Lepidoptera	*Ostrinia furnacalis*	Development time	Latitude (4)	No	7	[50]
		Growth rate		No		
Lepidoptera	*Heteronympha merope*	Development time	Latitude (5)	CoGV	3	[51]
		Growth rate		CoGV		
Lepidoptera	*Loxostege sticticalis*	Development time	Latitude (3)	No	4	[52]
Lepidoptera	*Colias eurytheme*	Feeding rate	Altitude (2)	Generalist-specialist and horizontal	5–6	[33]
Lepidoptera	*Colias eriphyle*	Feeding rate	Altitude (2)	Horizontal	10	[33]
Coleoptera	*Lilioceris cheni*	Development time	Latitude[b] (2)	No	4	[53]
Coleoptera	*Colaphellus bowringi*	Development time (larval)	Latitude (6)	CoGV	6	[54•]
		Development time (pupal)		No		
		Growth rate		CoGV		
Orthoptera	*Melanoplus femurrubrum*	Development time	Latitude (4)	CnGV	3	[55••]
		Growth rate		CnGV		
		Consumption rate		CnGV		
Orthoptera	*Melanoplus sanguinipes*	Development time	Altitude (3)	Horizontal	3	[56]
Hymenoptera	*Pachycrepoideus vindemiae*	Development rate	Latitude[c]	No	8	[57]
Odonata	*Coenagrion puella*	Growth rate (larval)	Urbanisation (6)	CnGV	5	[58•]
		Development time (egg)		No		

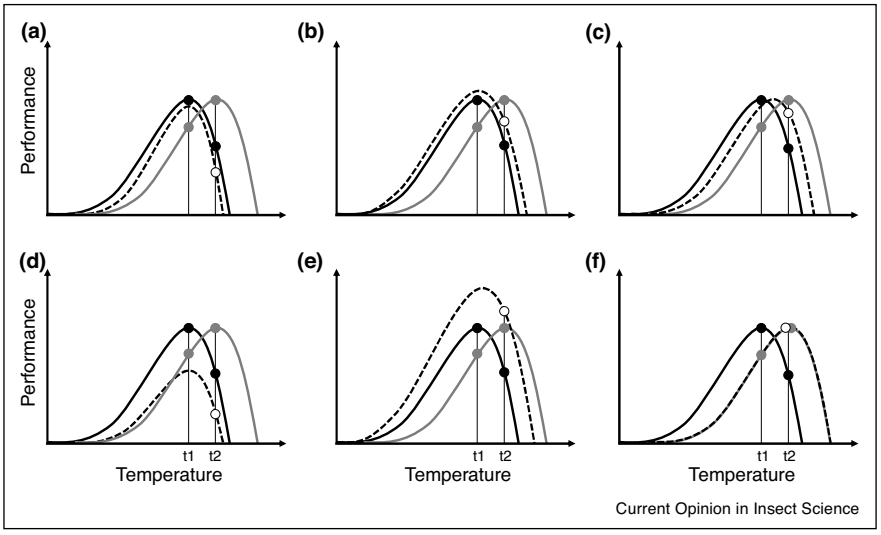
[a] The CnGV pattern was between central and southern populations, but not between central and northern population.
[b] Authors defined the two populations as biotypes, and do not mention a latitudinal gradient.
[c] Authors did not explicitly define the gradient as latitudinal, but as microclimatic.

species A will improve its performance at t2 compared to a situation where its TPC does not evolve (Figure 2b), and may even evolve a higher performance than species B if the magnitude of shifting is strong enough (Figure 2e). A final pair of evolutionary scenarios assumes a horizontal shift of the TPC of species A. Under a moderate horizontal shift, species A will improve its performance at t2 compared to a situation where its TPC does not evolve (Figure 2c). If the magnitude of horizontal shifting is strong enough, species A may even evolve the same performance as species B (Figure 2f).

Current studies using TPCs to predict biotic interactions under future warming

Empirical studies that incorporated spatial patterns in (and associated evolution of) TPCs of interacting species to

Figure 2



Conceptual diagrams of some hypothetical combinations of thermal performance curves (TPCs) of two interacting species, illustrating how evolutionary shifts in the TPC of one species may shape the outcome of the interaction between the two species. Species A (black) reaches its maximum performance at temperature t1, while species B reaches its maximum performance at t2. Dots located on the TPCs represent the performance of species A (black or white) and species B (grey) at the given temperature (t1 or t2). The two species outperform each other when located in their optimal thermal environment; that is, the black dot is higher than the grey dot at t1, and vice versa at t2. The dashed black lines represent the new TPC of species A after evolution, assuming evolution matches a common geographic scenario of TPC shifting (based on Figure 1). Six evolutionary scenarios are shown that differ in the direction and magnitude of the evolutionary shift of the TPC of species A. The six scenarios match moderate **(a)** and strong **(d)** countergradient variation, moderate **(b)** and strong **(e)** cogradient variation, and moderate **(c)** and strong **(f)** horizontal shifting of the TPC. Note that these simplified scenarios assume identical TPC shapes for the two species, and no evolution of the TPC of species B.

predict the outcome of their interaction under warming are extremely rare (but see [11] for a study with tunicates and bryozoans). Instead, fragmentary pieces of information exist. The many studies on geographic variation in TPCs (Figure 1) did not explicitly consider biotic interactions. Further, it has been widely documented that trophic interactions can show strong spatial patterns (for insects: [34–36]). Yet, these patterns are often attributed to density-related changes, and have not been linked to geographic differentiation in (thermal) performances. Other studies predicted species interactions in the face of future climates based on current TPCs (see below), yet ignored evolution and did not make a link to geographic patterns in TPCs. One notable exception is the conceptual framework put forward by Sternberg and Thomas [37••], where they simulated changes in TPCs (relevant for long-term interactions) to predict how local adaptation may alter responses of vector-borne diseases to climate warming.

The biotic interaction types best studied in the context of future warming that integrated TPCs are those between hosts and their parasites/parasitoids [38••,39,40,41••], as well as host–symbiont interactions [42]. Although these interactions are driven by more factors than the here studied performance traits, and these studies often measure traits relevant for long-term interactions (e.g. population growth rate), applying the insights obtained above is still relevant. A recent review comparing key TPC parameters (T_{opt}, CT_{min}, CT_{max}) for development rate between insect hosts and their parasitoids reported lower T_{opt} in parasitoids than their hosts, suggesting parasitoids to be more vulnerable to increasing temperatures relative to their hosts [40]. This was further supported by a follow-up study where the effects of climate change on host–parasitoid interactions were modelled using the diamondback moth *Plutella xylostella* and its parasitoid *Diadegma semiclausum* [40]. Similar findings were derived from a modelling study using TPCs (of reproduction and lifespan) of a reef-dwelling crab and its rhizocephalan parasite, predicting reduced parasitism with future warming [43••]. Although providing extremely valuable insight, both modelling studies ignored the potential of evolution changing the TPCs under warming. As indicated by the review summarized in Figure 1, this matches the 'no shift' scenario that indeed is common. Yet, in many cases TPCs have been shown to evolve along spatial gradients. The distinct, sometimes opposing hypothetical outcomes (demonstrated in Figure 2) highlight the importance of considering evolution of TPCs when predicting the dynamics of biotic interactions under climate change. This highlights that TPC evolution has the potential to strongly modify and even reverse the outcome of the interactions between hosts and their parasite/parasitoids under future warming compared to predictions by the models assuming no evolution.

Conclusions and future directions

Our review on recent insect studies identified that in many cases TPCs do not show geographic differentiation along strong thermal gradients, suggesting TPCs of these species will not evolve *in situ* under warming. Yet, in many other cases, a geographic signal was detected, mainly taking the forms of CnGV, and to a lesser extent CoGV and horizontal shifts. Hypothetical scenarios showed that in such cases taking evolution of the TPC into account may have a very strong impact on the predicted outcome of biotic interactions under warming. Moreover, besides the type also the magnitude of the TPC shift was identified to be crucial to determine who will be winners and losers. Unfortunately, current case studies that predicted effects of future warming based on TPCs did not consider evolution. Our results indicate that integrating information on geographic variation in TPCs when modelling the outcome of interactions would be an important step in increasing realism when predicting how biotic interactions will change under future climate change.

Conflict of interest statement

Nothing declared.

Acknowledgements

This work was supported by Belspo project Speedy, the KU Leuven Centre of Excellence program PF/2010/07, FWO research grant G.0524.17 and FWO scientific network EVE-net. Comments by Adam Rosenblatt and an anonymous reviewer greatly improved this paper.

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